Production Biology of Phytoplankton

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LONG-TERM GOALS

I continue to critically and creatively review knowledge about interactions between bulk marine phytoplankton and zooplankton with the hydrographic and chemical environment, as well as the feedback from the biological processes to the abiotic environment. The emphasis is on general principles, tests of the so-called canonical wisdom, and regional oceanography in the Arabian Sea.

OBJECTIVES

1. *To note the principal reason for the poor correlation between measured photosynthetic carbon uptake and draw-down of carbon dioxide over periods $\geq$ 24 h.* Iron scarcity is the ultimate reason for the occurrence of the High Nitrate-Low Chlorophyll (HNLC) regions that cover about 1/5 of the oceans, but it can occur also in coastal upwelling regions. For almost 15 years, the assumption has been that added iron would lead to growth of phytoplankton with material uptake (= draw-down) of carbon dioxide and influx of the gas from the atmosphere, hopefully followed by sedimentation of the newly formed organic matter and reduction of atmospheric carbon dioxide. Major open-sea, true experiments (iron fertilization patches compared with controls) have been undertaken during the last decade. It has, however, often been neglected that the draw-down of carbon dioxide was very much smaller than the measured uptake of carbon by the phytoplankton. I show for the two U.S. experiments in the eastern tropical Pacific that the reason was the grazing loss, which even during a quickly developing phytoplankton bloom (due to removal of the iron limitation) is very large indeed: far more than half, up to 9/10, of the newly assimilated carbon was regenerated during the same 24 h (see Results and Papers, Banse [2]). Out of this work grew a comment on routinely measuring ^{14}C uptake at sea (see Results and Papers, Banse [3]]).

2. *To study sources of variability in satellite-derived estimates of phytoplankton production*. A major goal for using maps of satellite-derived plankton chlorophyll is to estimate primary production, with the biogeochemical implications for estimating downward transport of organic matter and carbon dioxide exchange with the atmosphere (cf. the U.S. JGOFS program). To this day, however, the satellite-based estimates do not achieve a really useful accuracy as shown by comparison with in-situ measurements of photosynthesis (e.g., C.R. McClain et al., 2002, Deep-Sea Res, II 49: 2533-2560, for the tropical Pacific). One issue is the chlorophyll-normalized light-saturated photosynthetic rate being required for accuracy which, however, cannot yet be determined from space. Our approach is to

simulate satellite pigment and correlate it with simultaneously determined, existing in-situ photosynthesis (see Results, Banse & Postel [1]).

3. *To study the ventilation of the upper thermocline in the northernmost Arabian Sea.* Improved ventilation is due to convective overturn caused by the dry and cold northeast monsoon, which leads to a hitherto not widely recognized formation of high-density (sigma-t ~ 25 g dm^{-3}) water and sinking to up to ~ 150 m depth. A manuscript is nearing completion (see Results, Banse & Postel [2]).

4. *To continue the attempt to open windows to a largely unknown oceanographic literature* by arranging publication of translations of small monographs by Russian-language authors, as well as of a newly commissioned work by Russian-language (Ukrainian) authors (see Work Completed and Papers [4-6]).

WORK COMPLETED

A comprehensive paper about the phytoplankton in the offshore region between the southwest coast of India and the Laccadive Archipelago to the west has been published (Lierheimer & Banse 2002 [Publications, 1]). A paper on the role of grazing in the open sea is in press, as is a note on the use and limitation of the ^{14}C method (both by Banse [Publications, 2, 3]). A manuscript on a problem about estimating photosynthesis from satellite-derived pigment is essentially completed and the results were presented at a meeting (Results, Banse & Postel [1]). A manuscript on the hydrography of the northernmost Arabian Sea is advanced enough so that principal results were also presented at a meeting (Results, Banse & Postel [2]). The publication of the monographs translated from the Russian language, however, has not progressed. Three manuscripts (Sazhina; Pavlova; Banse & Piontkovski [Publications, 4-6]) languish, in part already for a year, at the press in Hyderabad (Deccan) or the Indian Academy of Sciences. The academy is supposed to conduct the scientific review and serve as the conduit of a printing subsidy from the Dept. of Ocean Development (DOD) in New Delhi. I have not been able to obtain non-contradictory answers for the reason(s) for the delay of type-setting the first volume and the delay in approval of the other two, although rumors have it that the DOD wants to (or has) renege(d) on the subsidy.

RESULTS

K. Banse, *Steemann Nielsen and the zooplankton* (Publications, [2]). Abstract: E. Steemann Nielsen is remembered by most biological oceanographers and limnologists as having introduced the ^{14}C method for measuring photosynthesis in 1952. The present paper is to recall that he was interested in the phytoplankton as part of the plankton community and was much aware of the role of grazing in affecting, if not determining, the concentrations of phytoplankton and, thus, also its rate of production. His principal statements to this effect were made with the open, oligotrophic subtropical and tropical oceans in mind where phytoplankton concentrations show little seasonal change. This paper is to show that Steemann Nielsen's sentiment also applies to non-static situations, especially phytoplankton blooms. Of the blooms in Cushing's North Sea *Calanus* patches of 1949 and 1954 and the two low-latitude, open-sea iron fertilization experiments (IronEx I, II) of the 1990s, more than half or even most of the newly formed cells were lost daily. In these examples, the same water was revisited, mixing was considered, and sinking was an unimportant loss term, so that grazing was the principal cause of mortality. Moreover, the examples show that over the course of the blooms, the rate and even the sign of temporal change of phytoplankton abundance had little relation to the rate of cell division, as already postulated by Riley's 1946 model of the seasonal cycle of phytoplankton on Georges Bank.

Thus, in most situations in the open sea and, presumably, large lakes, the rates of cell division (*instead* of photosynthesis by itself) *and* of mortality (most often from grazing) are needed for understanding and predicting the temporal change of phytoplankton abundance, a principal goal of biological oceanography. The mechanism maintaining the actual abundance of phytoplankton in the quasi-steady state prevailing over most of the ocean much of the time is still unclear.

K. Banse, *Should we continue to measure ^{14}C uptake by phytoplankton for another 50 years* (Publications, [3])? Abbreviated text: A principal goal of ecology and, hence, biological oceanography and limnology is to understand and be able to predict the abundance of organisms and the rate of temporal change. Can we achieve this goal for the phytoplankton by only measuring photosynthesis? My answer is NO, because (a) the rate of photosynthesis does not equal cell division, (b) phytoplankton is always accompanied by grazing zooplankton, and (c), the predictive power of measured ^{14}C-uptake toward the stated goal is small. In presenting the case, I restrict myself to the rate of temporal change but do not address the maintenance of concentrations. I consider time scales of $\geq$24 h and focus on ^{14}C-uptake, which for 50 years has been the method of choice for estimating photosynthesis in the open sea because of its sensitivity and ease of use (E. Steemann Nielsen 1952, J. Cons. 18: 117-140). To simplify the argument, the ^{14}C-uptake is assumed to represent net photosynthesis. The great utility of the method for, e.g., physiological studies is not considered.

Regarding (a), even the chlorophyll-normalized rate of photosynthesis, which is routinely used for modeling, is not the rate of cell division; we need also the chlorophyll-to-carbon ratio, which to this day is almost routinely overlooked in the planning of field work.

Regarding (b), year-round in about half of the warm oceans that is oligotrophic, and seasonally in a further few tens of percent, phytoplankton concentrations do not change for months on end although the cells divide roughly once a day. It has been shown that the balance is maintained by mortality which, as far as it is known, is principally due to grazing. Much of the efforts by phytoplankton workers, however, is not devoted to oligotrophic settings, but to non-equilibrium situations, e.g., the temperate and high-latitude spring blooms or the effects of fertilization on phytoplankton and CO_2 flux. They are generally understood as being resource-driven. Certainly, the location and timing of blooms are determined by bottom-up processes, but it turns out that the daily mortality even of exponentially increasing phytoplankton is very high. From revisiting of the same, marked water and comparing the cumulative gain of cells (or ^{14}C uptake) with the observed change of concentrations, or from simultaneously measuring cell division and grazing (dilution method), it is found after accounting for physical losses (mixing) that the majority of newly formed cells vanish every day by grazing (see review by Banse, in press). On the time scale considered, the high rate of photosynthesis (^{14}C-uptake) has little to do with the biological part of the small CO_2 flux into or out of the water because of the remineralization by the grazing.

Regarding (c), suppose we had determined today the chlorophyll-normalized ^{14}C-uptake (often called the assimilation number). Can we *mechanistically* predict from today's rates the ones prevailing tomorrow, even if we know the underwater irradiance and the nutrient concentrations? The answer here also is NO, since tomorrow's chlorophyll concentrations are not known, i.e., since we do not know how much of today's new growth (chlorophyll) will be left by tomorrow morning.

The conclusion: The concentrations of phytoplankton and the rate of change cannot be understood just from resource-controlled cell division rates, let alone photosynthesis. Likewise, the biologically-caused CO_2 flux into or out of the water cannot be found from photosynthesis alone. Instead, a mechanistic explanation (if not conceptual constructs) and prediction require consideration of grazing as a principal loss term in most spatial and temporal situations. However, as phytoplankton is never met without grazers, so the grazers are always a part of a community and exposed to their predators. Therefore, it is rarely, if ever, appropriate to study purely bottom-up (resource-) control or top-down (predation-) control of phytoplankton in the open sea. As far as the headline of this note is concerned: for the next half century, think about what you are going to do with the data before you gather them!

K. Banse & J.R. Postel (1). *On using pigment-normalized, light-saturated carbon uptake with satellite-derived pigment for estimating column photosynthesis.* (Symposium on *Phytoplankton Productivity, an Appreciation of 50 Years of the Study of Production in Oceans and Lakes*. Bangor [Wales], 19-22 March 2002). Abstract: Observed column photosynthesis (P_t, mg C m^{-2} d^{-1}, from ^{14}C uptake) may correlate only loosely with satellite-estimated phytoplankton pigment content at the same stations. We examine data from a meridional section astride the equator, a zonal section, as well as seasonal data from a fixed station, in the subtropical central North Pacific Gyre, and coastal upwelling during spring and summer off northern California and Washington. We correlate the observed P_t with the pigment that a satellite would have measured (C_{sat}, mg m^{-3}), simulated from in-situ data of chlorophyll (chlor. *a* + pheopigment). The correlation between predicted and observed P_t may or may not be improved by combining C_{sat} with the estimated light-saturated rate of photosynthesis, P^b_{opt} (mg C [mg chlor. *a* x d]$^{-1}$) for the particular station, as well as environmental variables. Incorporating P^b_{opt}, however, seems always to enhance the accuracy of the prediction of P_t. P^b_{opt} cannot be determined from space, but using geographic or seasonal means for the same data sets leads to imprecise and inaccurate correlations between predicted and observed P_t, principally because P^b_{opt} and P_t are often correlated. We expect this error source to be wide-spread. Further, the satellite-derived daily photosynthetic rate cannot predict the rate for the next day, because much or most of the newly assimilated carbon is being lost to grazing the same day. Therefore, next day's pigment concentration is unknown and, hence, photosynthesis or production cannot be calculated with useful accuracy. Over weekly or longer time scales, data assimilation from repeated pigment maps seems to be the solution.

K. Banse & J.R. Postel. *The "North Arabian Sea High Salinity Water" annually ventilates the upper part of the pycnocline north of 21-22°N.* (AGU/ASLO *"Ocean Sciences Meeting"*, Honolulu, HI, 11-15 February 2002; EOS Suppl. 83 [4]: 65). Abbreviated abstract: The salinity maximum in the northern Arabian Sea poleward of 21-22°N at or slightly deeper than the 25 g dm^{-3} isopycnal, which K.B. had mentioned in 1968 and described in 1984, is being revisited, principally based on seasonal coverage along five sections each between May 1975 and November 1976. Geographically, this "North Arabian Sea High Salinity Water" (NASHSW) replaces the Arabian Sea High Salinity Water of several authors that is present throughout the central and eastern Arabian Sea at ~ 24 g dm^{-3}. The water mass is apparently renewed annually by winter-time convection. Between 1960 and 1999, the NASHSW was observed at and above ~ 22° N in 21 out of 22 years with data and during the same period, also farther to the south. As a result, the oxygen content between 21-22 and 24-25°C is higher by 1-2 ml l^{-1} than in the open sea to the south. At ~20°C in the upper part of the oxygen minimum, the O_2 concentrations are twice or more than those to the south.

IMPACTS

1. The two papers by K. Banse (in press [2, 3]) about the role of zooplankton grazing are another attempt to get the notion across that mechanistic explanations and the prediction of the concentrations and the temporal changes of phytoplankton, as well as the draw-down of CO_2 during blooms, must be

sought in the context of the plankton as a community, with bottom-up and top-down processes almost always acting together. The paper or note by Banse (3) will in October 2002 reach a "captive" audience of > 3,000 colleagues.

2. The demonstration of an in part unpredictable correlation of satellite-derived pigment with phytoplankton production is another example of the needed continual testing of the canonical wisdom.

3. The translation of the two Russian monographs (4, 5) and the newly commissioned book are to open windows to a large body of literature that is largely unknown among English-only speaking scientists. Sazhina's and Pavlova's monographs also will be useful for work on freshwater plankton. The book about the Ukrainian expedition (Banse and Piontkovski, eds.[6]) and the data now made available on a CD will allow three-dimensional modeling, which is not easily attempted (if at all) based on the JGOFS sections of the mid-1990s. Moreover, the study will be a time-mark for 1980; without such points-in-time, we cannot establish whether or not the ocean is changing.

RELATED PROJECTS

Collaboration with colleagues at India's National Institute of Oceanography in Goa and the Central Marine Fisheries Research Institute in Cochin continues. Starting in mid-November, I will again spend 2 1/2 months with teaching and research in Goa, this time being financed by India. The research focus is on the stability on the decadal scale and the short-term variability of the offshore oxygen minimum of the Arabian Sea and on the near-bottom oxygen concentration on the shelf of the Indian west coast during the southwest monsoon using existing data.

PUBLICATIONS

(1) L.J. Lierheimer & K. Banse (2002) *Seasonal and interannual variability of phytoplankton pigment in the Laccadive (Lakshadweep) Sea as observed by the Coastal Zone Color Scanner.* Proc. Indian Acad. Sci. (Earth Planetary Sci.) 111: 163-185 (for abstract, see last year's report).

(2) K. Banse (in press) *Steemann Nielsen and the zooplankton.* Hydrobiologia (for abstract, see Results).

(3) K. Banse (in press) *Should we continue to measure ^{14}C uptake by phytoplankton for another 50 years?* ASLO (Am. Soc. Limnol. Oceanogr.) Bulletin 11 (3), October 2002 (for abstract, see Results).

(4) L.I Sazhina (translation in press; Russian original, 1987) *Reproduction, Growth, and Production of Marine Copepods.* With 35 figures and 55 tables (listed in FY2001 report). Universities Press (India), Hyderabad.

(5) E.V. Pavlova (translation submitted; Russian original, 1987) *Movement and Energy Metabolism of Marine Planktonic Organisms.* With 60 figures and 41 tables. Universities Press (India), Hyderabad.

(6) K. Banse & S.A. Piontkovski (contributors and editors; submitted) *Synoptic Ecosystem Structure of the Upper Layers of the Open Northwestern Arabian Sea during the Northeast Monsoon of 1990*. With 184 figures and 29 tables. Universities Press (India), Hyderabad (for abstracts of items [4-6], see the FY2001 report).